# Response of vegetation and carbon fluxes to brown lemming herbivory in Northern Alaska

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10 Abstract. The warming of the Arctic is affecting the carbon cycle of tundra ecosystems. Most research on carbon fluxes from 11 Arctic tundra ecosystems has focused on abiotic environmental controls (e.g. temperature, rainfall, or radiation). However, Arctic 12 tundra vegetation, and therefore the carbon balance of these ecosystems, can be substantially impacted by herbivory. In this study 13 we tested how vegetation consumption by brown lemmings (Lemmus trimucronatus) can impact carbon exchange of a wet-sedge 14 tundra ecosystem near Utgiagvik, Alaska during the summer, and the recovery of vegetation during a following summer. We 15 placed brown lemmings in individual enclosure plots and tested the impact of lemmings' herbivory on carbon dioxide (CO<sub>2</sub>) and 16 methane (CH<sub>4</sub>) fluxes and the normalized difference vegetation index (NDVI) immediately after lemming removal and during the 17 following growing season. During the first summer of the experiment, lemmings' herbivory reduced plant biomass (as shown by 18 the decrease in the NDVI) and decreased net CO<sub>2</sub> uptake, while not significantly impacting CH<sub>4</sub> emissions. CH<sub>4</sub> emissions were 19 likely not significantly affected due to CH<sub>4</sub> being produced deeper in the soil and escaping from the stem bases of the vascular 20 plants. The summer following the lemming treatments, NDVI and net CO<sub>2</sub> fluxes returned to magnitudes similar to those observed 21 before the start of the experiment, suggesting recovery of the vegetation, and a transitory nature of the impact of lemming herbivory. 22 Overall, lemming herbivory has short-term but substantial effects on carbon sequestration by vegetation and might contribute to 23 the considerable interannual variability in CO<sub>2</sub> fluxes from tundra ecosystems.

## 24 1 Introduction

25 The Arctic is warming at about three times the rate of the global average (IPCC, 2021), impacting tundra vegetation and the carbon 26 cycle. Vegetation influences the carbon stored in the tundra ecosystem through the exchange of carbon dioxide  $(CO_2)$  and methane 27  $(CH_4)$  from the soil into the atmosphere via respiration or by  $CO_2$  uptake through photosynthesis. One of the largest natural 28 reservoirs of organic carbon in the world is stored within Arctic soils, containing approximately 1,300 Pg of soil organic carbon 29 (Hugelius et al., 2014). Once soils thaw, microbes can convert stored carbon into greenhouse gases that enter the atmosphere, 30 contributing to global warming (McGuire et al., 2009; Schuur et al., 2008). This positive feedback could have dramatic effects on 31 warming rates, and these effects are why most carbon cycle research in tundra systems focuses on abiotic controls on carbon fluxes 32 (Kwon et al., 2019; Oechel et al., 2014; Sturtevant et al., 2012; Zona et al., 2010). Most of the studies investigating the patterns 33 and controls on the carbon balance from Arctic ecosystems focused on the environmental controls on CO<sub>2</sub> and CH<sub>4</sub>, while 34 overlooking the role of herbivory. Since herbivores remove photosynthetic tissues of vegetation, herbivory should substantially 35 decrease the ability of vegetation to photosynthesize and sequester CO<sub>2</sub> (Metcalfe and Olofsson, 2015). The decrease in vascular plant cover should also decrease CH<sub>4</sub> emissions, given that aerenchyma in sedges (Carex aquatilis is the dominant vascular plant 36 37 and sedge in our study site; Davidson et al., 2016) facilitate the escape of CH4 from deeper anoxic soil layers into the atmosphere

(Dias et al., 2010; McEwing et al., 2015; Ström et al., 2003; Whiting and Chanton, 1993). In addition to transport, vascular plants
also affect the release of labile carbon from photosynthetic tissues, which in turn stimulates CH<sub>4</sub> emission (Bhullar et al., 2014;
McEwing et al., 2015; Ström et al., 2003; Tan et al., 2015). Investigating the impacts of herbivory on Arctic vegetation and its
recovery after herbivory would contribute to a refined understanding of the response of tundra ecosystems to climate change.

42 Small rodents, especially lemmings, in the Arctic tundra of Alaska are important herbivorous consumers of plants and prey species for larger animals (Le Vaillant et al., 2018). Throughout the Arctic, few rodent species persist, of which lemmings are by 43 44 far the most abundant and widespread, and are consequently identified as keystone species in tundra environments (Krebs, 2011). 45 As dominant year-round grazers in the tundra, lemmings may heavily impact plant productivity (Olofsson et al., 2014). The site of our research, Utqiagvik, Alaska, was an ideal site for studying the impact of lemmings on vegetation, as it has been reported that 46 47 brown lemmings (Lemmus trimucronatus) deplete 100 times more primary production than caribou, a much larger herbivorous 48 mammal that migrates throughout the Alaskan Arctic (Batzli et al., 1980). Due to their life history characteristics and abundance, 49 lemmings can have a significant influence on the surrounding environment. Lemmings experience cyclic population dynamics 50 where their population density oscillates, changing community interactions (Soininen et al., 2017). Lemming grazing during 51 population peaks can dramatically affect vegetation (Olofsson et al., 2012), and therefore greenhouse gas fluxes from Arctic tundra; 52 given the amount of vegetation consumed by lemmings, their presence could have substantial impacts on the carbon balance of 53 tundra ecosystems. However, despite the role of lemmings as keystone herbivores, the direct impact of their vegetation 54 consumption on the carbon cycle of Arctic tundra in Alaska is still largely unknown, with few published studies evaluating the role 55 of lemming herbivory on the Arctic carbon balance and vegetation (Lara et al., 2017; Lindén et al., 2021; Metcalfe and Olofsson, 2015; Min et al., 2021). 56

Most of the studies analyzing the effects of lemmings on vegetation focused on ecosystem functioning in the absence of lemmings (Lara et al., 2017; Lindén et al., 2021; Min et al., 2021), the impacts of lemming waste products and carcasses on nutrient cycling and vegetation (McKendrick et al., 1980; Roy et al., 2020), the disturbance to soil via turnover by burrowing and fecal production (McKendrick et al., 1980), and recruitment and loss of forest vegetation (Ericson, 1977). This leaves a crucial gap in our understanding of how one of the main herbivores in a rapidly changing ecosystem, such as the Arctic, may affect carbon cycling. Since population cycles vary by species and region (Reid et al., 1995), qualitative predictions on how brown lemmings would alter Arctic vegetation and carbon cycling are uncertain.

In this study, we used enclosures to directly quantify impacts of lemming herbivory on tundra carbon cycling, both immediately after disturbance and during the growing season following the disturbance to examine vegetation recovery after one year. Thus far, very few studies (Johnson et al., 2011; Lara et al., 2017; Lindén et al., 2021; long-term exclosures) have investigated the effect of lemming herbivory on the tundra carbon cycle, including the timing of recovery of vegetation after lemming disturbance. By using enclosures to manipulate the number of lemmings per plot and observe a direct impact of lemming presence during peak annual activity, our study quantified the short-term effects of vegetation removal from lemming herbivory on carbon fluxes and the timing of vegetation recovery in the Alaskan Arctic.

The short-term effects of brown lemmings' herbivory on Arctic vegetation and carbon fluxes and their longer-term recovery are critical to understand how lemmings might influence tundra environments. For this purpose, we measured the impact of brown lemmings on vegetation in summer 2018 across a variety of plots in a wet-sedge tundra ecosystem in the Alaskan Arctic. Then, in summer 2019, we measured the plots again to evaluate vegetation recovery from lemmings' grazing. The goal of this experiment was to understand: (1) how brown lemmings affect vegetation through herbivory and disturbance, and therefore how they could impact the Arctic tundra carbon cycle and photosynthetic capacity of vegetation, and (2) the rate of vegetation recovery after brown lemming herbivory. We hypothesized that lemmings, given their high rate of vegetation consumption, would have a negative impact on net  $CO_2$ sequestration by vegetation, but due to the rapid regrowth of the annual vascular plants they preferentially consume, the vegetation would fully recover in terms of biomass and  $CO_2$  sequestration the growing season following grazing. We expected  $CH_4$  emission to decrease in response to herbivory, given the reduction in the biomass of vascular plants. Our broader goals are to increase our understanding of how the foraging behaviors of these herbivores impacts  $CO_2$  and  $CH_4$  fluxes and the photosynthetic capacity of plants in the Alaskan Arctic environment, which we hope will further public interest in the understanding of complex interactions in the Arctic and relationships that may exist between climate change, herbivory, and predator-prey interactions.

#### 85 2 Materials and methods

# 86 2.1 Study location

This study was carried out in Utqiaġvik (formerly Barrow), Alaska (Fig. 1a). Located in the Arctic Coastal Plain, Utqiaġvik is comprised of polygonal ground (flat-, low-, and high-center ice-wedge polygons) that cover roughly 65 % of the land cover (Billings and Peterson, 1980). The major vegetation type at this site is graminoid-dominated wetlands, consisting of mosses, lichens, graminoids (grasses), and wet sedges (Davidson et al., 2016).

The study area was located near the Barrow Atmospheric Baseline Observatory, an atmospheric monitoring site managed by the National Oceanic and Atmospheric Administration (NOAA) (Fig. 1b), approximately 2 km south of the Arctic Ocean (71°19′21.10″ N: 156°36′33.04″ W). This site was near a pre-established remote flux and meteorological tower monitored by the Global Change Research Group (Goodrich et al., 2016) and has substantial lemming populations relative to other Arctic tundra

95 areas in Alaska (Ott and Currier, 2012).



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97 Figure 1. (a) The location of the study site, Utqiaġvik (Barrow), in Alaska (© Google Maps 2018, imagery from TerraMetrics) represented by a 98 red star, (b) location of the sampling site (© Google Maps 2018, imagery from TerraMetrics), (c) distribution of the sampling plots on an image 99 created using the coordinates of the plots in R (Worldview-3 panchromatic imagery taken 24 July 2016, Maxar Technologies), (d) chamber used 100 for the greenhouse gas flux measurements, (e) chamber covered by light-blocking material, and (f, g) enclosures installed at each of the plots

101 during the manipulation experiment.

#### 102 2.2 Brown lemmings as a study species

Within the Arctic ecosystem of Alaska there are two species of lemmings: brown lemmings (*L. trimucronatus*) and northern collared lemmings (*Dicrostonyx groenlandicus*). Brown lemmings tend to be distributed among lower and middle Arctic tundra subzones (Stenseth, 1999). Although both brown and collared lemmings are found in Utqiaġvik, brown lemmings are more abundant in this region due to their preference for wetter habitats with relatively high-quality vegetation from lowlands (Batzli et al., 1983). Northern collared lemmings occupy drier habitats, and as a result are not as profuse and influential on vegetation in wet regions of the Alaskan Arctic such as Utqiaġvik (Batzli et al., 1983; Krebs et al., 2011; Morris et al., 2000).

## 109 2.2.1 Brown lemming consumption

110 Brown lemmings mostly consume graminoids in the summer and mosses in the winter (Batzli and Jung, 1980). Brown lemmings 111 can consume much more than predicted by general trends of terrestrial vertebrates (EPPO, 1994), consuming up to eight times their body weight each day (Stenseth and Ims, 1993). Thus, their extreme capacity for consumption, combined with their cyclic 112 113 elevated population densities in the region, can result in high vegetation removal. Additionally, during winter lemmings destroy or uproot up to 90-100 % of surrounding aboveground biomass within their foraging range (Stenseth and Ims, 1993). Arctic vegetation 114 consumed by lemmings is generally nutrient-poor (Batzli et al., 1980). Brown lemming digestive efficiency tends to be low, 115 digesting only about 30 % of ingested food (Batzli et al., 1980). Due to consistent year-round activity and their small body size, 116 lemmings also have a high metabolic rate. Low nutrient content, low digestive efficiency, and a high metabolic rate result in 117 lemmings requiring a high rate of food intake for survival. 118

To reduce the risk of detection by predators (snowy owl, parasitic jaeger/arctic skua, arctic fox, and ermine), lemmings forage on small areas near their burrows and maximize their foraging in these areas until their primary food source is depleted, at which point they move to a new area of vegetation near a burrow or runway (Erlinge et al., 2011). This behavior shapes their foraging habits and leads to a higher concentration of grazing on vegetation close to burrows and runways (Erlinge et al., 2011). As a result, approximately 95-100 % of graminoid shoots are repeatedly clipped by lemmings occupying burrows and visiting runways in the immediate vicinity of the vegetation, and as the distance from the burrows and runways increases, clipping becomes patchier and the intensity of clipping on vegetation decreases (Batzli et al., 1980).

# 126 2.2.2 Brown lemming population

Populations of brown lemmings tend to reach peak densities every three to five years and then steeply decline (Stenseth, 1999). Interactions between lemming populations as fast-growing consumers and plant populations as slowly recovering resources represents a bitrophic system (Ims and Fuglei, 2005). In this system, vegetation could be heavily damaged by overgrazing during peak years of lemming abundance.

A report on the monitoring of lemming abundance and distribution (Ott and Currier, 2012) estimated brown lemming density near Utqiaġvik in 2012 to range from five to 65 lemmings per hectare. However, basic population density estimates may underestimate the impact lemmings have on some vegetation due to an increased concentration in grazing very close to burrows and runways (Erlinge et al., 2011). Ott and Currier (2012) also used baited Sherman traps to estimate abundance, a live-trapping technique that may lead to an underestimate of the actual population density for this species, as brown lemmings are not readily recaptured using baited Sherman traps; we found manual capture techniques to be much more effective than baited traps.

# 137 2.3 Sampling plan and experimental design

138 We performed this experiment over two summer growing seasons. During the first season (summer 2018), we used enclosures to 139 ensure even lemming herbivory pressure in each of our experimental plots. We manually captured the lemmings used in this first 140 season shortly after peak growing season (3-10 August), coinciding with accelerated lemming reproduction and peak population 141 density. We captured the lemmings in close proximity to our sampling sites while conducting visual encounter surveys, and secured 142 them in Sherman traps with cotton nestlets and vegetation (grasses and sedges). Our samples included both juvenile and adult life 143 stages. We released or avoided capturing any sick, very slow, or noticeably pregnant lemmings. After capture, we relocated 144 lemmings to the study site and included them in the experimental plots. Like voles (close relatives of lemmings), lemmings have 145 distinct preferences for habitats containing their preferred food items (Batzli and Henttonen, 1990), which we specifically selected 146 for when designing the location of the experimental plots in this study in order to represent realistic effects of lemming herbivory. 147 We established 10 plot sets for this experiment. Each of the 10 plot sets included a lemming plot paired to a control (no-148 lemming) plot nearby (20 plots in 10 sets total) (Fig. 1c). Each plot contained the different vegetation types, mosses, lichens, 149 graminoids, and wet sedges, and was selected to be as similar to the other plot within the same set as possible in order to minimize 150 biases due to spatial heterogeneity in vegetation and other landscape characteristics influencing vegetation and carbon fluxes (a 151 more in-depth analysis of these vegetation types was completed by Davidson et al. in 2016). We placed plot sets approximately 3 152 m apart from each other. Control plots were located within 1 m of lemming plots in the same set to keep environmental factors as 153 similar as possible. Plots were 50 x 50 cm in size; in each plot we dug a galvanized hardware cloth with a  $\frac{1}{2}$  inch grid down through the thawed soil to the permafrost and up to 60 cm above the surface (Fig. 1f and g). We selected the size of these plots to be 154 155 consistent with a similar lemming exclosure experiment by Eskelinen and Virtanen (2005) in Finland. This size is also similar, yet 156 a bit larger than the experimental plots in the study by Lara et al. (2017) near Utqiagvik, Alaska which used 30 x 30 cm chamber 157 bases within their exclosures. Control plots not only excluded lemmings for the duration of the experiment, but also served as a 158 control for the soil and vegetation disturbance resulting from digging galvanized hardware cloth into the soil. Plots that included 159 lemmings also included a top portion of hardware cloth that prevented lemmings from escaping via climbing and prevented 160 predators from removing the lemmings during the experiment. Inside each enclosure with a lemming was a locked-open Sherman 161 trap with cotton nestlets for protection from environmental elements.

162 Because rodents may experience physiological stress after being captured (Fauteux et al., 2018a), prior to the experiment we 163 kept the lemmings in small individual cages made of hardware cloth with a locked-open Sherman trap for shelter, cotton nestlets 164 for warmth, and vegetation for nutrition for at least an hour to help them acclimate. After this acclimation period, we placed the 165 lemmings in their individual plots for 16 hours. We based the duration of the experiment on field trials we carried out for several 166 weeks before the start of the experiment. These trials showed that 16 hours was enough time to observe an average impact on the 167 vegetation, visually similar to the effect lemmings have on areas near their burrows, but was not too long as to result in complete 168 vegetation consumption, unrepresentative of most areas where lemmings forage. Our field trials revealed that keeping lemmings 169 inside the enclosure for longer than 16 hours (which varied with lemming size) led to a complete vegetation removal, an extreme scenario only observed in the very close proximity of the burrows, and not representative of most of their foraging areas. We 170 171 released the lemmings at the end of all these experiments in proximity to the locations where they were captured.

The subsequent season (summer 2019), we re-visited the sample plots to measure the impact of lemmings one year after their grazing (24 June-7 August). During this season, we did not capture any lemmings, nor did we perform any additional manipulation. To be able to assess longer-term impacts of the manipulations carried out the previous summer, we collected measurements throughout the following summer (Table 1) to represent pre-, early, and peak growing season (hereafter defined as "rounds"). Sampling was carried out to monitor the timing of regrowth of photosynthetic tissue and recovery of the plants at different times

- 177 of the season in 2019: 24-29 June (round one: pre-growing season), 9-19 July (round two: early growing season), and 29 July-7
- 178 August (round three: peak growing season).
- 179

	Data Collected	Frequency of Measurement
Summer	$CO_2$ fluxes (NEE) and $CH_4$ fluxes,	Before (pre-herbivory) and after (post-herbivory) lemming treatment
2018	NDVI, air temperature, soil	(N=10 before and N=10 after for each treatment, for a total of N=40
	temperature, soil moisture, thaw depth,	per NEE, CH <sub>4</sub> fluxes, NDVI; N=40 for air temperature; N=40 for soil
	motion camera footage	temperature; N=100 for soil moisture; N=20 for thaw depth)
Summer	CO <sub>2</sub> fluxes (NEE, ER, GPP) and CH <sub>4</sub>	Different times of the season (pre-, early, peak growing season)
2019	fluxes, NDVI, air temperature, soil	(N=10 for each round and treatment, for a total of N=60 per NEE, ER,
	temperature, soil moisture, thaw depth	GPP, CH <sub>4</sub> fluxes, NDVI; N=60 for air temperature; N=300 for soil
		temperature: $N=240$ for soil moisture: $N=240$ for thaw depth)

180 Table 1. Types of data collected and when they were measured during summer 2018 and summer 2019. All data were collected while lemmings 181 were not present inside the experimental plots, except for the motion camera footage. NEE is defined as net ecosystem exchange, ER as ecosystem 182 respiration, GPP as gross primary production, and NDVI as the normalized difference vegetation index.

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There could have been other sources of herbivory (such as caribou), but these sources are not as frequent in these northernmost areas of the Arctic Coastal Plain. Additional sources of disturbance to vegetation could originate from a drastic change in environmental conditions, such as extreme temperatures, extremely dry conditions, etc.; however, these would not selectively remove the vascular plants while not affecting the moss layer, which is what we observed in this experiment.

## 188 2.4 Greenhouse gas fluxes and environmental variables measurements

189 We used a Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyzer (UGGA Model 915-0011) to measure CO<sub>2</sub> and  $CH_4$  concentrations (currently, global mean atmospheric concentrations for  $CO_2$  and  $CH_4$  are approximately 417 ppm and 1909 190 191 ppb, respectively; NOAA GML, 2022) and air temperature over time in all plots during both summer seasons (2018 and 2019). 192 We measured CO<sub>2</sub> and CH<sub>4</sub> concentrations one day after lemming removal from the plots in summer 2018 (exact time varied based 193 on weather conditions and when plots were measured in temporal relation to other plots) and during the different rounds of the 194 growing season in summer 2019. To collect measurements, we built a clear plexiglass acrylic chamber (Davidson et al., 2016; 195 McEwing et al., 2015) to enclose the plots once the aboveground portion of the caging had been detached and the lemming had 196 been removed (Fig. 1d). This chamber was placed on a metal frame positioned in the ground outside of the plots and had clear polyvinyl material weighed down by heavy metal chains to produce a seal inside the chamber. These measurements were performed 197 in a closed loop, where tubes connected the chamber to the gas analyzer and then air was circulated back to the chamber. We 198 199 positioned a small fan inside the chamber to ensure appropriate air mixing. We collected greenhouse gas concentrations in the 200 absence of lemmings.

We used the rate of concentration change to calculate carbon fluxes using the chamber volume and area covered by vegetation (i.e. responsible for the carbon emission or uptake) as a function of time, as described in McEwing et al. (2015). The CO<sub>2</sub> concentration change allowed us to calculate the net balance between the carbon uptake from photosynthesis and the carbon loss from respiration, also defined as the net ecosystem exchange (NEE), before and after manipulations as previously described (summer 2018) and to track the seasonal development of NEE during the following summer (2019). In the subsequent summer (2019), we used a light-blocking material to cover the chamber (Fig. 1e) for determining CO<sub>2</sub> ecosystem respiration (ER) and gross primary production (GPP) from NEE, calculated following Eq. (1):

 $208 \quad GPP = NEE - ER ,$ 

(1)

and using the sign convention suggested by Chapin et al. (2006). Since plant growth and photosynthetic uptake is restricted to the summer months in these Arctic ecosystems, we used GPP to indicate "the total amount of  $CO_2$  'fixed' by land plants per unit time through the photosynthetic reduction of  $CO_2$  into organic compounds" (Gough, 2011) during the time of measurements, rather than as an annual measurement.

We also measured a variety of environmental variables before and after each portion of the experiment (summer 2018) and during each round (summer 2019). These environmental variables included air temperature recorded by the LGR gas analyzer, soil temperature measured with a Thomas Scientific Traceable Kangaroo thermometer, soil water content recorded by a FieldScout Soil Moisture Meter, and thaw depth using a metal probe marked every 5 cm. We examined these variables as controls that may explain shifts in  $CO_2$  and  $CH_4$  fluxes within the study area and to monitor if plots in each of the sets were experiencing similar abiotic conditions. This assured potential differences in carbon fluxes were due to our manipulation, and not different environmental conditions of various plots.

## 220 2.5 Camera footage and hyperspectral measurements

We quantified the impact of lemming herbivory and burrowing on vegetation using a Spectra Vista Corporation (SVC) Spectroradiometer HR-512i, which measures spectral reflectance and records a picture of the vegetation being scanned. The spectrometer yielded hyperspectral measurements for vegetation in the 338.9-1075.1 nm spectral range with 512 bands and a bandwidth of  $\leq 1.5$  nm. We used the internal global positioning system (GPS) of the spectroradiometer to record geographic coordinates (latitude and longitude) for all plots to an accuracy of 2.5 m. We collected hyperspectral measurements in the absence of lemmings.

We measured total reflected spectral exitance from a blank white reference panel right before sampling each plot set (approximately every 20-30 scans, or 10-15 minutes) to estimate spectral irradiance based on reflectance calibration information provided for the reference panel. We recorded spectral surface reflectance before and after each experimental treatment (summer 2018) and at different times during the season in the following summer (2019) and used it to calculate narrow-band normalized difference vegetation index (NDVI) to compare the photosynthetic capacity of vegetation in the plots. NDVI is calculated as the normalized difference between reflectance in the near infrared wavelengths (800.5 nm) and red wavelengths (680.2 nm). Lower values of NDVI indicate no living vegetation and higher values indicate more green biomass.

We recorded a time-lapse of various parts of the experiment using a Brinno MAC200DN Outdoor Camera to collect motionsensor video footage of lemming activity. The camera also allowed for re-visitation and surface cover characterizations of the plots to classify and quantify vegetation types within each plot and assess how grazing had affected vegetation. We did not systematically record all trials on video, but instead used this technology as a qualitative tool to visually document the activity of the lemmings.

#### 238 2.6 Statistical analyses

We used the statistical program R, version 3.5.1 (R Core Team, 2019), for our statistical analyses. We tested for normality using a Shapiro-Wilk normality test. The 2018 data were normally distributed (NEE P = 0.489, NDVI P = 0.816), except the CH<sub>4</sub> data (P < 0.001), which were right-skewed, so we log-transformed the CH<sub>4</sub> data to help normalize them (P = 0.284). After this transformation, we used linear mixed-effects models (with the package "nlme"; Pinheiro et al., 2018) to test for the significance between the different treatments. For the 2019 data, we used both linear mixed-effects models and non-parametric Kruskal–Wallis tests because we could not make all the data normal using the same transformation method (log transformation, square root transformation) for every round during the season. We also tested for equal variance using an F-test and found there was no 246 significant difference between the variances (treatments) in 2018 (NEE P = 0.172, CH<sub>4</sub> flux P = 0.810, NDVI P = 0.100) and 2019 247 (NEE P = 0.441, ER P = 0.650, GPP P = 0.852, CH<sub>4</sub> flux P = 0.346, NDVI P = 0.951).

248 We tested multiple variations of the linear mixed-effects models using the methods for model selection in ecology described 249 in Zuur et al. (2009). We then plotted the models to examine the residuals of the data and found them to not appear heteroscedastic. 250 For the 2018 models, we used treatment (control, lemming plots), time (before, after experiment), and their interaction as fixed 251 factors in the models; for the 2019 models, we used treatment (control, lemming plots), round (pre-, early, and peak growing 252 season), and their interaction as fixed factors in the models. In all analyses we used the plot identification (1C, 1E, 2C, 2E, etc.) 253 nested within the plot set (1-10) as random factors. Mixed models allow us to account for temporal and spatial pseudoreplication 254 and to test the significance of the interactions among factors. When fixed factors were significant, we conducted a pairwise analysis 255 via a Tukey post-hoc test (with the package "emmeans"; Lenth et al., 2019) to investigate the interacting effects in the model.

To identify the effect of the manipulation on carbon fluxes and NDVI, we applied the linear mixed-effects models and tested for differences in each environmental variable before and after lemming exposure in summer 2018. We then used the statistical analyses to help us explore if the post-lemming experimental plots showed a significant change in carbon fluxes and NDVI when compared to pre-lemming experimental plots (2018), and if the carbon fluxes and NDVI varied between treatments the following growing season (2019). Our analysis of the NDVI from spectral indexes provided us with information on changes in plant biomass before and after each manipulation in summer 2018 and vegetation regrowth in summer 2019.

#### 262 3 Results

#### 263 3.1 Environmental variables

Environmental controls on CO<sub>2</sub> and CH<sub>4</sub> fluxes such as air temperature, soil temperature, thaw depth, and soil moisture were similar between the control and experimental plots in 2018 (Fig. A1a-h) and 2019 (Fig. A1i-p). During summer 2018, air temperature (P = 0.542), soil temperature (P = 0.960), thaw depth (P = 0.683), and soil moisture (P = 0.619) were not significantly different between control plots and lemming plots. During summer 2019, measurements of the control and lemming plots were not significantly different for air temperature (P = 0.887), soil temperature (P = 0.060), thaw depth (P = 0.512), and soil moisture (P= 0.387).

# 270 3.2 Carbon fluxes

271 The presence of lemmings significantly impacted  $CO_2$  fluxes (i.e. NEE) during summer 2018 when the lemming enclosure 272 treatment was implemented. Before the treatment, calculated NEE (Fig. 2a) and CH<sub>4</sub> fluxes (Fig. 3a) for the control and lemming 273 plots were similar. After we removed lemmings from experimental plots, net  $CO_2$  uptake decreased significantly (P < 0.001, Fig. 274 2a). In this context, net  $CO_2$  uptake by vegetation, or carbon dioxide sequestration, is the removal of  $CO_2$  from the atmosphere and 275 its storage in the above- and belowground biomass through photosynthesis after accounting for the carbon loss through respiration. 276 Therefore, when lemmings consume the photosynthetic tissues of the vegetation (aboveground biomass), the vegetation is no 277 longer able to uptake CO<sub>2</sub> from the atmosphere, and NEE (the net ecosystem exchange equivalent to the net CO<sub>2</sub> fluxes) approaches 278 either zero or becomes less negative (a negative sign implies more carbon removal from the atmosphere). By the end of summer 279 2018, the effect of brown lemmings' herbivory changed the mean NEE for lemming plots from  $-0.074 \pm 0.012$  gC-CO<sub>2</sub>m<sup>-2</sup>h<sup>-1</sup> (i.e. 280 net CO<sub>2</sub> sequestration) to  $0.003 \pm 0.012$  gC-CO<sub>2</sub>m<sup>-2</sup>h<sup>-1</sup> (i.e. net CO<sub>2</sub> fluxes were around zero). Contrary to what we expected, CH<sub>4</sub> 281 flux values did not significantly differ between control plots and plots subjected to lemmings' herbivory (P = 0.989, Fig. 3a).

282 In summer 2019, we measured NEE and CH<sub>4</sub> fluxes again, and additionally calculated ER and GPP. During this second summer of measurements, results of the linear mixed-effects models for NEE, ER, GPP, and CH<sub>4</sub> fluxes were all not significantly different 283 284 between control and lemming plots (NEE P = 0.834, Fig. 2b; ER P = 0.742, Fig. 4a; GPP P = 0.716, Fig. 4b; CH<sub>4</sub> flux P = 0.869, Fig. 3b). These results were consistent with those of the Kruskal-Wallis test, which found there was no significant difference 285 286 between the treatments in 2019, either by testing the data set all together (NEE P = 0.769, ER P = 0.221, GPP P = 0.513, CH<sub>4</sub> flux P = 0.824) or separating it for different times of the season (rounds) and testing each time separately (pre-growing season: NEE P 287 = 0.245, ER P = 0.672, GPP P = 0.296, CH<sub>4</sub> flux P = 0.728; early growing season: NEE P = 0.853, ER P = 0.600, GPP P = 0.558, 288 CH<sub>4</sub> flux P = 0.638; peak growing season: NEE P = 0.293, ER P = 0.366, GPP P = 0.212, CH<sub>4</sub> flux P = 0.970). 289



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Figure 2. Box and whisker plots of 2018 and 2019 NEE for the control and lemming plots. Negative flux values indicate carbon sequestration/uptake from the atmosphere by vegetation though photosynthesis and positive flux values indicate carbon emission/loss into the atmosphere. (a) Median NEE for plots before and after the experiment in summer 2018 (T = 4.62, P < 0.001), and (b) median NEE for plots during the three rounds of measurements in summer 2019 (T = 0.21, P = 0.834).



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Figure 3. Box and whisker plots of 2018 and 2019 CH<sub>4</sub> fluxes for control and lemming plots. Negative flux values indicate uptake from the atmosphere and positive flux values indicate emission to the atmosphere. (a) Median CH<sub>4</sub> flux for plots before and after the experiment in summer 2018 (T = 0.01, P = 0.989), and (b) median CH<sub>4</sub> flux for plots during the three rounds of measurements in summer 2019 (T = -0.17, P = 0.869).



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Figure 4. Box and whisker plots of ER and GPP for control and lemming plots during the three rounds of data collection in summer 2019. Positive flux values indicate a positive respiration (carbon loss into the atmosphere) and a positive carbon uptake by vegetation through photosynthesis. (a) Median ER (T = -0.34, P = 0.742), and (b) median GPP (T = -0.37, P = 0.716). The signs of ER and GPP are always positive, but if ER is more than GPP, then the ecosystem is a carbon source into the atmosphere (with a positive sign of NEE).

# 304 3.3 Hyperspectral surface reflectance and NDVI

Spectral reflectance derived from spectroradiometric radiances generally increased across visible and near infrared wavelengths after lemmings' vegetation removal (Supplementary Fig. S1). Before placing lemmings in enclosures, control and lemming plots exhibited similar surface reflectance values, while reflectance curves showed more substantial separation after lemming removal (Supplementary Fig. S1). Analyzing the surface reflectance of the same control and lemming plots re-visited in summer 2019 revealed that the reflectance values for these different treatments were alike in each plot set, similar to what was observed before the beginning of the manipulation experiment (Supplementary Fig. S2b).

To better quantify the changes in reflectance, we calculated the NDVI in all the control and treatment plots in both summer 311 312 2018 and 2019. Following lemming removal in the first summer, lemming plots had significantly lower NDVI than the control plots (P = 0.015, Fig. 5a), consistent with the decrease in green biomass observed in the photographs collected before and after 313 placing the lemmings in the treatments' enclosure (Supplementary Fig. S1), and with the decreases in net CO<sub>2</sub> uptake (see NEE 314 315 close to zero after lemming vegetation consumption; Fig. 2a). The effect of brown lemmings' herbivory changed the mean NDVI for lemming plots from  $0.551 \pm 0.021$  to  $0.465 \pm 0.021$ . During the second summer, median NDVI values of all plots were similar 316 317 (Fig. 5b). Results of the linear mixed-effects model reveals that during this time, there was no significant difference in NDVI when comparing control plots to lemming plots (P = 0.692), which is consistent with the results of the Kruskal–Wallis test that found 318 there was no significant difference between the treatments in 2019 either by testing the data set all together (P = 0.694) or separating 319 it for different times of the season (rounds) and testing each time separately (pre-growing season: P = 0.260, early growing season: 320 P = 0.418, peak growing season: P = 0.283). There was a significant difference in NDVI across the rounds (P < 0.001), which 321 coincides with the increased green biomass observed in collected photographs from pre- to early to peak growing season 322 323 (Supplementary Fig. S2a).



Figure 5. Box and whisker plots of 2018 and 2019 NDVI values for control and lemming plots. (a) Median NDVI for plots before and after the experiment in summer 2018 (T = -3.69, P = 0.015), and (b) median NDVI for plots during the three rounds of measurements in summer 2019 (T= 0.41, P = 0.692). Higher vascular plant green biomass in the pre-lemming treatment plots presented NDVI values in the 0.6 to 0.7 range, whereas post-lemming treatment plots in 2018 exhibit NDVI values around 0.5.

#### 329 4 Discussion

330 We found, within a short-term enclosure experiment, that brown lemmings' herbivory significantly decreased net CO<sub>2</sub> uptake 331 immediately after consumption of vegetation, while surprisingly not affecting CH<sub>4</sub> fluxes. Consumption of photosynthetically active plant tissue by lemmings impacted the ability of the vegetation to sequester CO<sub>2</sub>, nullifying CO<sub>2</sub> uptake by tundra vegetation. 332 333 The lack of significant difference in the evaluated environmental variables (air temperature, soil temperature, soil moisture, thaw 334 depth) between the control and lemming treatment plots suggests that these factors did not play a significant role in the difference 335 in net CO<sub>2</sub> fluxes before and after the treatments during the first summer. Unfortunately, the design of this experiment, mostly focusing on the aboveground measurements (except for the soil temperature, soil moisture, and thaw depth), did not allow for 336 337 identifying the contribution of belowground increased decomposition from the aboveground vegetation removal. However, as we 338 did not notice an increase in CH<sub>4</sub> emission with vegetation removal (which could have increased as an indirect effect of an increase 339 in sugars related to increased soil microbial respiration), we could assume that the direct effect of the removal of photosynthetic 340 plant tissue was the main mechanism explaining the decrease in the ability of the ecosystem to sequester carbon. Therefore, we believe that the removal of vascular plants from lemming herbivory was the main driver explaining the decrease in the ability of 341 342 these ecosystems to uptake carbon.

343 Notably, lemmings' herbivory did not affect  $CH_4$  fluxes, even though plant transport of  $CH_4$  is a critical pathway for emission 344 in tundra ecosystems (Lai, 2009; McEwing et al., 2015); plants offer substrate for methanogenesis and increase CH<sub>4</sub> transport 345 (Bridgham et al., 2013). The lack of a significant effect on  $CH_4$  fluxes may be due to the location of vegetation removal on consumed plants. Kelker and Chanton (1997) showed the location of the clipping of vegetation affects the CH<sub>4</sub> emissions; 346 belowground clipping at the root-shoot or porewater-root boundary is more likely to impact CH<sub>4</sub> emission, but aboveground 347 348 clipping is less likely to affect CH<sub>4</sub> emission. This differential effect is likely related to the location of CH<sub>4</sub> escape though 349 vegetation, which is just at the root-shoot or porewater-root boundary (Kelker and Chanton, 1997). Clipping has an effect not only 350 on gas transport, but also on substrate availability. Vegetation can have an impact on stimulating CH<sub>4</sub> through labile carbon exuded by the roots (McEwing et al., 2015; Ström et al., 2003; Zona et al., 2009). Labile carbon fuels methanogenesis, aiding in CH<sub>4</sub> 351 352 production in the Arctic (Tan et al., 2015). However, labile carbon as a result of root exudation depends on photosynthetic activity 353 of vegetation to be a controlling mechanism of  $CH_4$  emission (Bhullar et al., 2014; Ström et al., 2003). Thus, given the

photosynthetic activity of vegetation decreasing resulting from lemming consumption, it is likely that soil labile carbon did not have a crucial impact on  $CH_4$  emission in this study. The lack of response of  $CH_4$  emissions to vegetation removal could be explained by the large soil carbon stored in these permafrost soils (Hugelius et al., 2014). A decrease in labile carbon exudation due to vegetation removal from herbivory may have not been limiting  $CH_4$  emissions, consistent with a lack of response in  $CH_4$ emissions with a labile carbon addition in these sites (von Fischer et al., 2007).

Moreover, when measured shortly after the lemming treatment, the  $CH_4$  emission in the plots may have been inhibited by lemming urine. Ammonium from urine has been linked to an increase in  $CH_4$  production (Lin et al., 2009); however, it has been found that  $CH_4$  fluxes can initially result in a mean negative flux shortly after the addition of urine to the system (Boon et al., 2014). The timing in which we measured the greenhouse gases after the lemming treatments falls within the initial window of time found by Boon et al. (2014) to have this effect; thus, urine produced by the lemmings in the plots may have nullified the positive  $CH_4$  emissions via the aerenchyma. Without further investigation into the soil chemistry, it is difficult to determine which mechanisms of herbivore-plant interactions resulted in the lack of significance in  $CH_4$  emission.

366 Measurements collected the summer following our herbivory experiment (2019), revealed that the vegetation recovery after 367 brown lemming disturbance was rapid. In 2019, vegetation quickly regrew to a condition comparable to that found in 2018, prior 368 to lemming consumption. Since lemmings mostly consume vascular plants, such as graminoids and sedges, in the summer and 369 avoid non-vascular and slower growth vegetation, such as mosses and lichens (Batzli et al., 1980), the preferential consumption of annual grasses and sedges likely led to the rapid recovery of the photosynthetic capacity of vegetation we observed in just one 370 371 year. From analysis of the motion-sensor video footage, we observed lemming foraging within the plots was representative of these 372 vegetation preferences. An in-depth analysis of the vegetation types found in our plots was completed in a previous study by our 373 team (Davidson et al., 2016).

As expected, the biomass of vegetation decreased during summer 2018 due to the impact of lemming consumption (Supplementary Fig. S1). The control and experimental plots before the lemming treatment had relatively high and similar mean NDVI values (Supplementary Fig. S1), suggesting their biomass had similar values (Goswami et al., 2015). Vegetation removal by brown lemmings significantly lowered the mean NDVI of the plots subjected to lemming herbivory. By summer 2019, the mean NDVI value of these same lemming plots indicated that the vegetation was fully recovered from the lemmings' impact the previous summer.

380 While our experiment showed a potentially substantial impact of lemming herbivory on the CO<sub>2</sub> fluxes from these tundra 381 ecosystems, we did not address the impact of varying degrees of intensity of herbivory and population cycling of brown lemmings 382 on carbon fluxes and photosynthetic capacity of different vegetation communities. Roy et al. (2020) found that herbivore presence 383 can alter communities of vegetation differently, as herbivores play a role in regulating a variety of plant species. These herbivores 384 can lead to significant changes in the abundance of vegetation types, allowing for the potential of the tundra during the peak 385 growing season to switch between a carbon source to sink in the absence of herbivory (Min et al., 2021). Since brown lemmings rely on a high rate of food intake to sustain growth and reproduction (Batzli et al., 1980) and experience population cycles with 386 387 distinct seasonal and multiannual density fluctuations (Reid et al., 1995; Stenseth, 1999), rapid consumption of plant matter by lemmings as sustenance during population peaks may significantly contribute to shifts in plant communities and, thus, carbon cycle 388 389 changes.

Since lemming population densities vary in response to multiple environmental factors (Fauteux et al., 2015; Soininen et al., 2017), predicting a 'normal' level of herbivory for this species is very challenging. Reports on estimated brown lemming density have found their local density to range from five to 65 lemmings per hectare (Ott and Currier, 2012; Alaskan Arctic) and about zero to nine lemmings per hectare (Fauteux et al., 2015; Canadian Arctic), which is variable and may be an underestimate due to the use of live-trapping, as mentioned previously. Moreover, in addition to space, it is important to consider time: we only kept lemmings inside the plots for 16 hours and there was no effect of lemming herbivory for the remainder of the experiment. The most relevant comparison we could find to define the degree of herbivory observed was the effect on vegetation near lemming burrows and runways in a similar ecosystem (Erlinge et al., 2011; Siberian tundra). Given the sparsity of available literature and data from these understudied Arctic ecosystems, it is difficult to categorize our lemming treatment as having some sort of 'normal' or 'heavy' impact on vegetation, which would be required to explore legacy effects of lemming herbivory.

Lemming populations may also vary in response to regulation by predators (Fauteux et al., 2018b). Given the substantial impact of lemming herbivory on the tundra carbon balance, indirect cues indicating predatory risk could change lemming foraging behavior, and in turn alter their effect on vegetation. The influence of predator-prey interactions on herbivory, and how they further impact vegetation and carbon fluxes in the Arctic tundra should be quantified by future studies to better understand multifaceted interactions in the Arctic (see supplementary materials).

#### 405 5 Conclusions

406 We show that there is an immediate effect of lemmings on plant biomass and net CO<sub>2</sub> uptake by Arctic vegetation, but not on CH<sub>4</sub> 407 flux in areas where lemmings forage. However, impacts on vegetation are temporary, and plant biomass and net CO<sub>2</sub> uptake can 408 recover to previous conditions by the end of the subsequent growing season. To further our understanding of the complex 409 interactions in the Arctic, it is vital to also explore the longer-term feedbacks that may exist between climate change, herbivory, 410 and predator-prey interactions. The effects of warming on snow cover and plant growth, as crucial environmental resources to 411 lemmings, could lead to drastic population changes for lemmings, and the longer-term effect of lemmings' herbivory on vegetation might not be captured by a short-term manipulation. It is also critical to link the long-term lemming population fluctuations to 412 413 potential shifts in vegetation and climate change. Additionally, climate change is likely to also alter the abundance, behavior, or 414 even occurrence of predators of lemmings, which may in turn impact lemming abundance and foraging behaviors. For these 415 purposes, longer-term and broader scale ecological data would be particularly valuable to build on the short-term effect highlighted 416 in this study.

417 Overall, our study suggests that brown lemmings have the ability to significantly alter vegetation by consuming photosynthetic tissue, which hinders the sequestration by the vegetation and shifts CO<sub>2</sub> fluxes in the areas surrounding their burrows and runways. 418 419 We report that this effect is short-lived due to the preferential consumption by lemmings of plant species that quickly regrow and 420 recover by the next growing season. However, the duration of the impacts of lemming herbivory may change in different vegetation 421 communities, as various plant species might be affected differently. Thus, it is relevant to examine the effects of lemmings on a 422 wide range of ecosystems to make regional estimates of their short-term influence on net CO<sub>2</sub> fluxes and NDVI. Future research 423 should also more carefully quantify the interactions between lemmings, their predators, and carbon cycling in the Arctic tundra 424 ecosystem, which might explain some of the substantial interannual variability in the tundra CO<sub>2</sub> fluxes not explained by 425 environmental variables alone.

<sup>426</sup> *Code availability.* R codes generated for data analysis during this study will be archived to the ORNL DAAC repository by the corresponding 427 author upon the journal's request.

- 428 Data availability. Data on carbon fluxes, hyperspectral surface reflectance, and environmental variables analyzed during this study will be
- 429 archived to the ORNL DAAC repository by the corresponding author upon the journal's request. All relevant data are included as figures in the
- 430 paper, and raw data may be made available upon request.

431 Author contribution. Study conception and design were carried out by Jessica Plein, Rulon Clark, Walter Oechel, and Donatella Zona. Material 432 preparation, data collection, and data processing were completed by Jessica Plein. Data scripts and codes were written by Jessica Plein, Kyle 433 Arndt, and Donatella Zona. Data analysis was performed by Jessica Plein and Donatella Zona. The drafts of the manuscript were written by 434 Jessica Plein and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

435 *Competing interests.* The authors declare that they have no conflict of interest.

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- 443 Care and Use Committee (IACUC) Animal Protocol Form #16-08-014C.
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## 596 Appendix A







- 599 Figure A1. Box and whisker plots of environmental variables across treatment plots during (a-h) summer 2018 and (i-p) summer 2019.
- 600 Environmental variables include (**a**, **i**) air temperature for the entire dataset, (**b**, **j**) air temperature by plot, (**c**, **k**) soil temperature for the entire
- 601 dataset, (**d**, **l**) soil temperature by plot, (**e**, **m**) thaw depth for the entire dataset, (**f**, **n**) thaw depth by plot, (**g**, **o**) soil moisture for the entire dataset,
- 602 and (**h**, **p**) soil moisture by plot.